

Assessing Water Quality with Submersed Aquatic Vegetation

Habitat requirements as barometers of Chesapeake Bay health

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Worldwide, estuaries are experiencing water quality problems as a result of human population growth in coastal areas. Chesapeake Bay, one of the world's largest estuaries, has experienced deterioration of water quality from nutrient enrichment, sediment inputs, and high levels of contaminants, resulting in anoxic or hypoxic conditions and declines in living resources (Horton and Eichbaum 1991). A mechanism for relating anthropogenic inputs to the health of Chesapeake Bay is through determination of relationships among water quality and various living resources. In particular, the establishment of habitat requirements and restoration goals for critical species living in Chesapeake Bay is a way in which scientists, resource managers, politicians and the

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By establishing habitat requirements, scientists, managers, and the public can work toward a clean, healthy bay

public can work toward the goal of obtaining a clean, healthy bay (Funderburk et al. 1991).

We use habitat requirements of submersed aquatic vegetation to characterize the water quality of Chesapeake Bay because of their widespread distribution in the bay, important ecological role, and sensitivity to water quality parameters. Our primary goal is to synthesize information leading to the establishment of quantitative levels of relevant water quality parameters necessary to support submersed aquatic vegetation, a major resource of Chesapeake Bay (Batiuk et al. in press). The development of a habitat requirement approach for Chesapeake Bay could prove useful in other estuaries experiencing water quality degradation.

Submersed aquatic vegetation

Submersed aquatic vegetation is comprised of rooted flowering plants that have colonized primarily soft sediment habitats in coastal, estuarine, and freshwater habitats. In Chesapeake Bay, seagrasses in saline regions and freshwater angiosperms that have colonized lower-salinity portions of the estuary constitute a diverse (approximately 20 species) community of submersed aquatic vegetation (collectively known as SAV; Hurley 1990). Seagrasses are typically defined as the approximately 60 species of marine angiosperms (den Hartog, 1970); however, representatives of the several hundred species of freshwater macrophytes are often found in estuarine habitats (Hutchinson 1975). For the purpose of this article, the term *submersed aquatic vegetation* is used for both marine angiosperms and freshwater macrophytes that are found in Chesapeake Bay. These plants historically have been one of the major factors contributing to the high productivity of Chesapeake Bay (Kemp et al. 1984), especially the abundance of waterfowl.

During the last two decades, there has been an increasing recognition of the importance of submersed aquatic vegetation in coastal and estuarine ecosystems. Submersed aquatic vegetation provides food for waterfowl and critical habitat for shellfish and finfish. This vegetation also affects nutrient cycling, sediment stability, and water turbidity (reviewed in Larkum et al. 1990, McRoy and Helfferich 1977, Phillips and McRoy 1980). However, declines of submersed aquatic vegetation are being documented worldwide (Europe: Giesen et al. 1990; North America: Costa 1988, Orth and Moore 1983; Australia: Cambridge and McComb 1984) because of anthropogenic in-

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puts such as sediments and nutrients that affect the water quality of coastal ecosystems (Thayer et al. 1975).

In Chesapeake Bay, a large-scale decline of submersed aquatic vegetation occurred in the late 1960s and early 1970s (Orth and Moore 1983, 1984). This decline was related to increasing amounts of nutrients and sediments in Chesapeake Bay resulting from development of the bay's shoreline and watershed (Kemp et al. 1983, Twilley et al. 1985). Currently, there are approximately 25,000 ha of submersed aquatic vegetation in Chesapeake Bay (Orth et al. 1991), which is approximately 10% of its historical distribution (Stevenson and Confer 1978).

Submersed aquatic vegetation is particularly crucial as an indicator of water clarity and nutrient levels, because habitat requirements developed for various species of birds, fish, and shellfish in Chesapeake Bay do not incorporate these conditions (Funderburk et al. 1991). Habitat requirements of these other organisms instead focus on chemical parameters (e.g., dissolved oxygen, pH, salinity, toxic compounds, and temperature). Many of the restoration goals of birds, fish, and shellfish involve changes in both environmental quality and management of human harvesting activities. In contrast, submersed aquatic vegetation restoration goals can be linked solely to environmental quality, thus providing for more direct assessment of restoration progress.

The generic nature of submersed aquatic vegetation/light interactions leads to a potential for wider application of submersed aquatic vegetation habitat requirements. Establishment of minimal light requirements for various submersed aquatic vegetation species coupled with water quality monitoring data could be used to establish water clarity and nutrient standards in a variety of coastal environments with the goal of preventing further vegetation declines.

Minimal light requirements of submersed aquatic vegetation

Submersed aquatic vegetation requires light for photosynthesis, and its growth, survival, and depth penetration is directly related to light availability (Dennison 1987, Kenworthy

and Haunert 1991). The maximal depth at which submersed plants can survive increases with increasing light penetration, as measured with underwater surveys of plant distributions and a Secchi disc (Figure 1). The Secchi depth is the maximal water depth at which a black and white disc (30-centimeter diameter) can be seen from the surface. In spite of the differences between freshwater and marine submersed aquatic vegetation and their habitats (e.g., Stevenson 1988), the general relationships between light availability and depth penetration of submersed aquatic vegetation in various locations are similar in shallow, turbid waters (Secchi depth less than 5 m).

In deeper, clear waters (Secchi depth more than 10 m), a divergence between depth limit and Secchi depth occurs in freshwater versus marine habitats (Duarte 1991). The depth limit for angiosperms in freshwater habitats is 17 m, even at Secchi depths of 23 m (Figure 1a). In contrast, submersed aquatic vegetation in marine habitats tend to have depth limits that exceed the higher Secchi depths (Figure 1b). In Chesapeake Bay, Secchi depths are generally 1–2 m, and submersed aquatic vegetation are restricted to shallow water depths (less than 3 m at mean low water [MLW]).

Minimal light requirements for submersed aquatic vegetation are determined from simultaneous measurements of the maximal depth limit for submersed aquatic vegetation and the light attenuation coefficient. A conversion factor between Secchi depth and light attenuation coefficient can be used (Giesen et al. 1990). The percentage of incident light (photosynthetically active radiation [PAR] = 400–700 nm) that corresponds to maximal depth penetration of submersed aquatic vegetation is determined using a negative exponential function according to the Lambert-Beer equation:

$$I_z = I_0 \cdot e^{-K_d \cdot z}$$

where I_z is the PAR light at depth z , I_0 is the PAR light just below the water surface, K_d is the light attenuation coefficient, and z is the water depth. Assuming that the minimal light requirement is the light level at the maximal depth penetration (z), per-

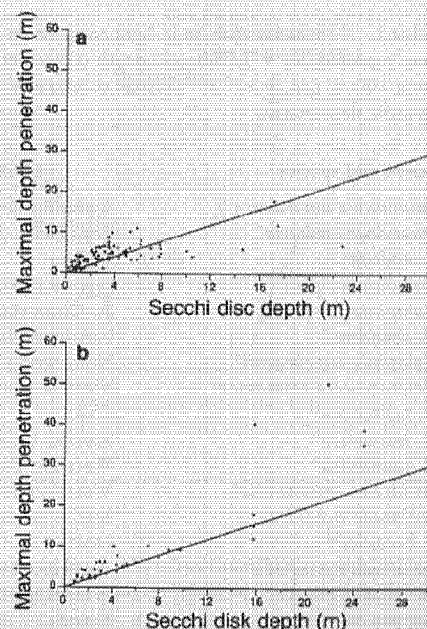


Figure 1. Maximal depth penetration of (a) freshwater macrophytes and (b) marine submersed aquatic vegetation plotted as a function of Secchi depth. The 1:1 line of maximal depth penetration and Secchi depth is plotted for reference. Freshwater data from Canfield et al. 1985 and Chambers and Kalff 1985; marine data from references listed in Table 1.

cent light can then be determined. In this manner, the average minimal light requirement for freshwater angiosperms from lakes in Canada was determined to be $21.4 \pm 2.4\%$ of surface light levels (Chambers and Kalff 1985), and the average minimal light requirement for marine submersed aquatic vegetation was 10.8% (Duarte 1991). However, there is a wide range of minimal light requirements among species (Table 1), likely a result of differences in physiological and morphological adaptations.

Overall, the minimal light requirements of submersed aquatic vegetation (4–29% of incident light measured just below the water surface) are much higher than those of other plants. Terrestrial plants from shade habitats have light requirements on the order of 0.5–2% of incident light measured at the top of the canopy (Hanson et al. 1987, Osmond et al. 1987). Both phytoplankton and benthic algae have minimal light requirements that are significantly less than those of submersed aquatic vegetation: charophytes, 2–3% (Sand-Jensen 1988); green algae, 0.05–1.0% (Luning and Dring 1979); brown al-

Table 1. Maximal depth limit, light attenuation coefficient (K_d), and minimal light requirements of various species of seagrass. Where Secchi depths were reported, $K_d = 1.65/\text{Secchi depth}$ (Giesen et al. 1990). Minimal light requirements were calculated as percent light at the maximal depth limit using $100 \times I_z/I_0 = e^{-K_d \cdot Z}$. Range of maximal depth limit and K_d values and means \pm SE of minimal light requirement given in locations with multiple data points.

Genus and species	Location	Maximal depth limit (m)	K_d : light attenuation coefficient (m^{-1})	Minimal light requirement (%)
<i>Amphibolis antarctica</i> *	Waterloo Bay (Australia)	7.0	0.20	24.7
<i>Cymodocea nodosa</i> *	Ebro Delta (Spain)	4.0	0.57	10.2
<i>C. nodosa</i> *	Malta	38.5	0.07	7.3
<i>Halodule wrightii</i> †	Florida (US)	1.9	0.93	17.2
<i>Halophila decipiens</i> ‡	St. Croix (US)	40.0	0.08	4.4
<i>H. decipiens</i> *	Northwest Cuba	24.3	0.10	8.8
<i>Halophila engelmanni</i> *	Northwest Cuba	14.4	0.10	23.7
<i>Heterozostera tasmanica</i> *	Victoria (Australia)	3.8–9.8	0.36–0.85	5.0 \pm 0.6
<i>H. tasmanica</i> *	Chile	7.0	0.25	17.4
<i>H. tasmanica</i> *	Spencer Gulf (Australia)	39.0	0.08	4.4
<i>H. tasmanica</i> *	Waterloo Bay (Australia)	8.0	0.20	20.2
<i>Posidonia angustifolia</i> *	Waterloo Bay (Australia)	7.0	0.20	24.7
<i>Posidonia oceanica</i> *	Medas Island (Spain)	15.0	0.17	7.8
<i>P. oceanica</i> *	Malta	35.0	0.07	9.2
<i>Posidonia ostenfeldii</i> *	Waterloo Bay (Australia)	7.0	0.20	24.7
<i>Posidonia sinuosa</i> *	Waterloo Bay (Australia)	7.0	0.20	24.7
<i>Ruppia maritima</i> *	Brazil	0.7	3.57	8.2
<i>Syringodium filiforme</i> *	Northwest Cuba	16.5	0.10	19.2
<i>S. filiforme</i> *	Florida (US)	6.8	0.25	18.3
<i>S. filiforme</i> ‡	Florida (US)	1.9	0.93	17.2
<i>Thalassia testudinum</i> *	Northwest Cuba	14.5	0.10	23.5
<i>T. testudinum</i> *	Puerto Rico	1.0–5.0	0.35–1.50	24.4 \pm 4.2
<i>T. testudinum</i> *	Florida (US)	7.5	0.25	15.3
<i>Zostera marina</i> §	Kattegat (Denmark)	3.7–10.1	0.16–0.36	20.1 \pm 2.1
<i>Z. marina</i> ¶	Roskilde (Denmark)	2.0–5.0	0.32–0.92	19.4 \pm 1.3
<i>Z. marina</i> *	Denmark	1.5–9.0	0.22–1.21	20.6 \pm 13.0
<i>Z. marina</i> *	Woods Hole (US)	6.0	0.28	18.6
<i>Z. marina</i> *	Netherlands	2.5	0.49	29.4
<i>Z. marina</i> *	Japan	2.0–5.0	0.38–0.49	18.2 \pm 4.5

*Duarte 1991.

†W. J. Kenworthy, personal communication, 1990.

‡Williams and Dennison 1990.

§Ostenfeld 1908.

¶Borum 1983.

gae, 0.7–1.5% (Luning and Dring 1979); crustose red algae, 0.0005% (Littler et al. 1985); and lacustrine and marine phytoplankton, 0.5–1.0% (Parsons et al. 1979, Wetzell 1975). Because there is a high minimal light requirement for submersed aquatic vegetation, its survival depends on good water clarity. Therefore, it is important to focus on light attenuation processes to explain the distributions of submersed aquatic vegetation.

The minimal light requirement of a particular species of submersed aquatic vegetation determines the maximal water depth at which it can survive. This relationship is depicted graphically as the intersection of the light intensity versus depth curve with the minimal light requirement (Figure 2). Light intensity is attenuated exponentially with water depth (Figure 2, right side). The minimal light requirement

of a particular submersed aquatic vegetation species, as a percentage of incident light, intersects the light curve to give a predicted maximal depth of survival for that species (Figure 2, left side). Light attenuation is temporally and spatially variable, and in the Chesapeake Bay study we used median values taken at monthly intervals during the growing season to characterize light attenuation. Maximal depth limits of submersed aquatic vegetation are less temporally variable, with time intervals of months to years before changes are observed; consequently, annual surveys are generally made.

Minimal light requirements are consistent for each species of submersed aquatic vegetation, with little variation within species (Table 1). The differences in temporal variability of light attenuation, maximal depth limit, and minimal light requirements

often results in an imbalance in relative accuracy of these parameters. Knowledge of two of these three unknowns (average light attenuation coefficient [K_d], minimal light requirement, or maximal depth of submersed aquatic vegetation survival) allows determination of the remaining unknown. For example, an assessment of the maximal depth penetration of the seagrass *Zostera marina* with knowledge of its minimal light requirement (Table 1) allows for the determination of an average light-attenuation coefficient. In this manner, depth penetration of submersed aquatic vegetation is used as an integrating "light meter" to assess light regimes on the appropriate temporal and spatial scales (with respect to survival) without intensive sampling programs (cf. Kautsky et al. 1986).

Light attenuation within the water column is a function not only of the

water itself, but also of its dissolved and particulate components, which serve to reflect, refract, absorb, and scatter the incident radiation (Figure 3). Particulate organic and inorganic particles are washed in from surrounding uplands or resuspended from bottom deposits and can severely limit light penetration in shallow waters. Inorganic nutrients enhance the growth in the water column of phytoplankton as well as epiphytic algae, which absorb light before it reaches the leaf surface of submersed vegetation. The spectral character of the light may also be changed so that attenuation is greatest in the photosynthetically important blue and red wavelengths of the visible spectrum (Champ et al. 1980, Pierce et al. 1986), thereby placing additional stress on submersed aquatic vegetation growth and survival. Thus, light availability is a function of a complex interaction of factors that are directly or indirectly related to water quality, including factors not included in the conceptual model (e.g., dissolved organic matter).

In spite of this complexity, it should be possible to predict submersed aquatic vegetation growth and survival from the known levels of certain key water-quality parameters or, conversely, to predict long-term water quality levels based on the distribution of submersed aquatic vegetation if the levels of the factors that adversely affect submersed aquatic vegetation are known. This approach does not rely on a complete understanding of the water-quality interactions affecting light attenuation but rather on empirical data on water quality and survival of submersed aquatic vegetation.

Chesapeake Bay submersed vegetation

To determine the critical water-quality values that correspond to submersed aquatic vegetation survival, water-quality gradients along subestuaries of Chesapeake Bay were compared to patterns of transplant survival and distributions of submersed aquatic vegetation. We base our analysis of these relationships on case studies of different regions of Chesapeake Bay, by different investigators over several years. Four study

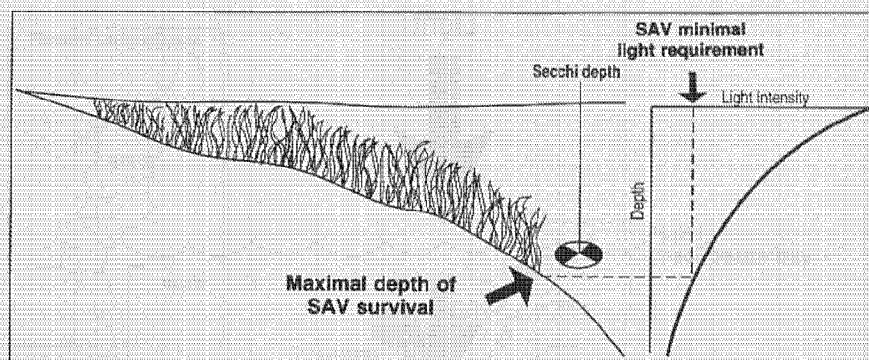


Figure 2. Determination of maximal depth of submersed aquatic vegetation (SAV) survival by the intersection of minimal light requirement and light attenuation curve (% of surface light).

areas were used: upper Chesapeake Bay, upper Potomac River, Choptank River, and York River (Figure 4). These areas represent regions of intensive study in the past decade where data on water quality and submersed aquatic vegetation growth were available. The areas span the salinity regimes of Chesapeake Bay: tidal fresh (0–0.5 ‰), oligohaline (0.5–5 ‰), mesohaline (5–18 ‰), and polyhaline (18–25 ‰).

The upper Chesapeake Bay, which includes the Susquehanna Flats and the Elk, Sassafras, Northeast and Susquehanna rivers, is a region with tidal freshwater and oligohaline areas. This area historically supported some of the most extensive submersed aquatic vegetation populations in Chesapeake Bay in the 1950s and 1960s (Bayley et al. 1978, Davis 1985). Although there are no precise records on distributions during this period, there are 11,100 ha of bottom that could potentially support submersed aquatic vegetation (less than 2 m water depth MLW). Yet, now only 20% of this area has submersed aquatic vegetation, much of which is sparse (Orth et al. 1991). A variety of species are found in this region, principally *Vallisneria americana*, *Ceratophyllum demersum*, *Potamogeton* spp., and *Najas* spp., along with the exotic species *Myriophyllum spicatum*.

The upper Potomac River is also characterized by tidal freshwater and oligohaline waters. Historically, this section had abundant submersed aquatic vegetation through the 1930s (Carter et al. 1985, Cumming 1916, Jaworski et al. 1972). However, subsequent declines left the area nearly devoid of submersed aquatic vegeta-

tion until 1983 (Haramis and Carter 1983). Increased water clarity, a result of improvements in sewage treatment and unusual weather conditions, caused a resurgence of submersed aquatic vegetation beginning in 1983. A diverse submersed aquatic vegetation community (13 species) developed, including the exotic species *Hydrilla verticillata* (Carter and Rybicki 1986). Currently, 2,500 ha are vegetated, dominated by *H. verticillata*, *M. spicatum*, and *V. americana* and representing approximately 19% of the river bottom less than 2 m water depth (MLW; Carter and Rybicki 1990, Orth et al. 1991).

The Choptank River is the largest tributary on the eastern shore of the Chesapeake Bay, with mesohaline to tidal freshwater reaches. It was estimated that 15,000 ha of the Choptank River was vegetated with *Ruppia maritima*, *Zannichellia palustris*, *M. spicatum*, and several species of *Potamogeton* in the 1960s (Stevenson and Confer 1978). However, in 1990 a single species (*R. maritima*) occupied only 190 ha (Stevenson et al. in press), approximately 1% of Choptank River bottom less than 2 m water depth (MLW; Orth et al. 1991).

The York River is one of the five major tributaries on the western shore of the Chesapeake Bay, with the study area in the polyhaline and mesohaline reaches. Abundant submersed aquatic vegetation consisting of *Zostera marina* and *R. maritima* was found along the shoals of this river in 1971, covering 820 ha (Orth and Gordon 1975). Decline of these species occurred in the 1970s, principally in the upriver and deep water portions of the beds. By 1990, significant regrowth of sub-

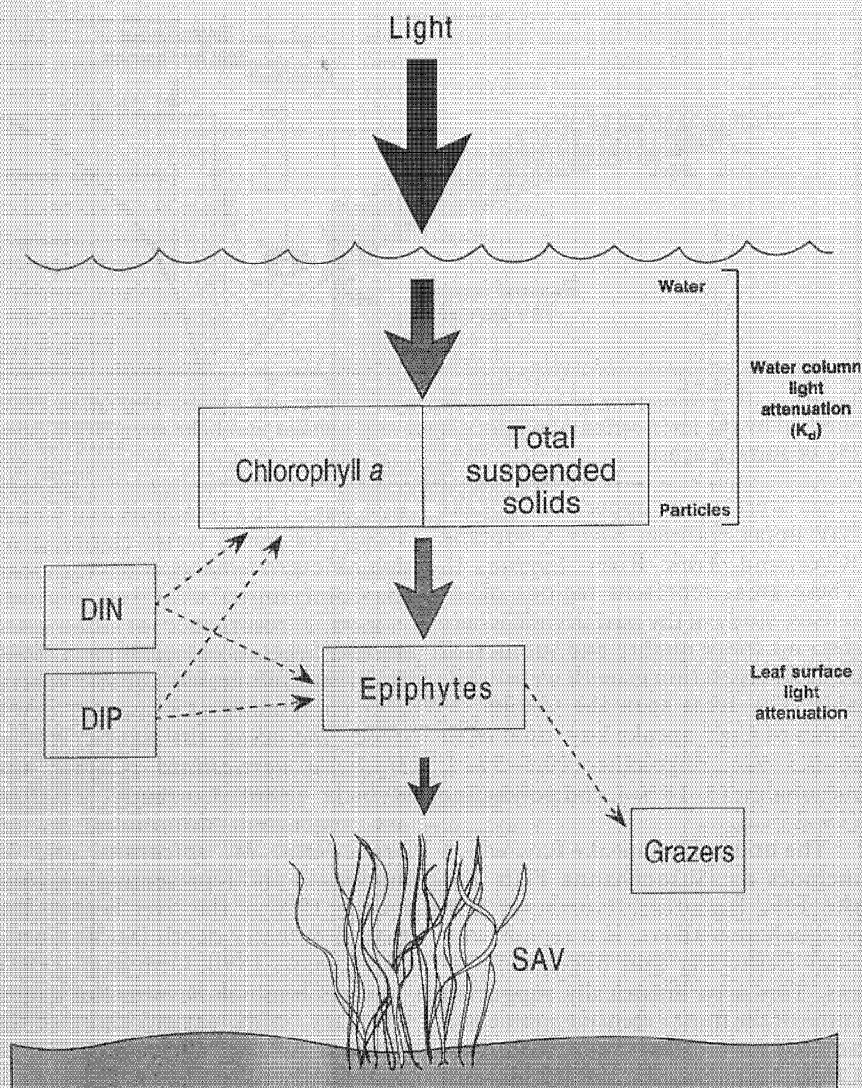


Figure 3. Availability of light for submersed aquatic vegetation (SAV) is determined by light attenuation processes. Water column attenuation, measured as the light attenuation coefficient (K_d), results from absorption and scatter of light by particles in the water (phytoplankton, measured as chlorophyll a , and total organic and inorganic particles, measured as total suspended solids) and by absorption of light by water itself. Leaf surface attenuation, largely due to algal epiphytes growing on submersed leaf surfaces, also contributes to light attenuation. Dissolved inorganic nutrients (DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus) contribute to phytoplankton and epiphyte components of overall light attenuation, and epiphyte grazers control accumulation of epiphytes.

Table 2. Chesapeake Bay submersed aquatic vegetation habitat requirements. For each parameter, the maximal growing season median value that correlated with plant survival is given for each salinity regime. Growing season defined as April–October, except for polyhaline (March–November). Salinity regimes are defined as tidal fresh = 0–0.5 ‰, oligohaline = 0.5–5 ‰, mesohaline = 5–18 ‰, polyhaline = more than 18 ‰.

Salinity regime	Light attenuation coefficient (K_d ; m^{-1})	Total suspended solids (mg/l)	Chlorophyll a ($\mu g/l$)	Dissolved inorganic nitrogen (μM)	Dissolved inorganic phosphorus (μM)
Tidal freshwater	2.0	15	15	—	0.67
Oligohaline	2.0	15	15	—	0.67
Mesohaline	1.5	15	15	10	0.33
Polyhaline	1.5	15	15	10	0.67

mersed aquatic vegetation had occurred, primarily in the downriver areas, with upriver areas still unvegetated. Currently, approximately 15% of York River bottom less than 2 m water depth (MLW) is covered with submersed aquatic vegetation (Orth et al. 1991).

The habitat requirements approach

Habitat requirements for submersed aquatic vegetation are defined as the minimal water-quality levels necessary for survival. Survival was defined by the presence of either fluctuating or persistent vegetation beds or the survival of transplants of submersed aquatic vegetation. Areas with persistent beds were defined as areas where submersed aquatic vegetation survived across multiple growing seasons. Areas with fluctuating beds were defined as areas where vegetation was present for one growing season or less or where there appeared to be significant shifts in interannual distribution and abundance patterns.

Water-quality parameters used in the delineation of habitat requirements were chosen because of their availability in water-quality data sets and their relevance to submersed aquatic vegetation survival. Yet, other parameters also affect survival, and the selected parameters are not independent variables. Some degree of interdependence of these parameters is illustrated by three-dimensional plots of total suspended solids, chlorophyll a , dissolved inorganic nitrogen, dissolved inorganic phosphorus, and light attenuation coefficient (Figure 5). But, these parameters were not highly correlated using a Pearson's correlation analysis of all parameters for the data in Figure 5, analyzing separately stations with and without submersed aquatic vegetation (Batiuk et al. in press). Correlations (r) between parameters were all less than 0.5 except for K_d x total suspended solids ($r = 0.76$ and $r = 0.74$ in areas with and without seagrass, respectively) and K_d x chlorophyll a ($r = 0.54$ in areas with submersed aquatic vegetation). The lack of appreciable correlation for most of the parameters supports the use of multiple habitat requirements to better predict survival of submersed aquatic vegetation.

Empirical relationships between water-quality characteristics and distributions of submersed aquatic vegetation provided the means of defining habitat requirements for vegetation survival. Habitat requirements were formulated by determining vegetation distributions by transplant survival and bay-wide distributional surveys, measuring water-quality characteristics along large-scale transects that spanned vegetated and unvegetated regions, and combining distributional data and water-quality levels (as in Figure 5) to establish the minimal water quality that supports submersed aquatic vegetation survival.

This correspondence analysis was strengthened by factors common to each of the case studies. Field data were collected over several years (almost a decade in the Potomac River) in varying meteorologic and hydrologic conditions by different investigators. Submersed aquatic vegetation distributions in the four case studies across all salinity regimes were responsive to the five water-quality parameters used to develop habitat requirements. In addition, interannual changes in water quality led to changes in submersed aquatic vegetation distribution and abundance in each region that were consistent with habitat requirements.

Habitat requirements

Water-quality conditions sufficient to support survival, growth, and reproduction of submersed aquatic vegetation to water depths of one meter below MLW were used as habitat requirements (Table 2). One-meter water depth was chosen because present-day Chesapeake Bay submersed aquatic vegetation beds are generally restricted to one meter (MLW) or less. For submersed aquatic vegetation to survive to one meter, light attenuation coefficients less than 2 m^{-1} for tidal fresh and oligohaline regions and less than 1.5 m^{-1} for mesohaline and polyhaline regions were needed. Measurements of total suspended solids (less than 15 mg/l) and chlorophyll *a* (less than $15 \text{ } \mu\text{g/l}$) were consistent for all regions. The close similarity in habitat-requirement values identified for total suspended solids, chlorophyll *a*, and light attenuation coefficient (K_d) for all salinity regimes of Chesapeake Bay suggests that growth and survival of submersed aquatic vegetation, regardless of their location and species at those locations, all respond to these water-quality parameters within a small range of values. This correspondence may allow for an overall baywide management strategy for these parameters.

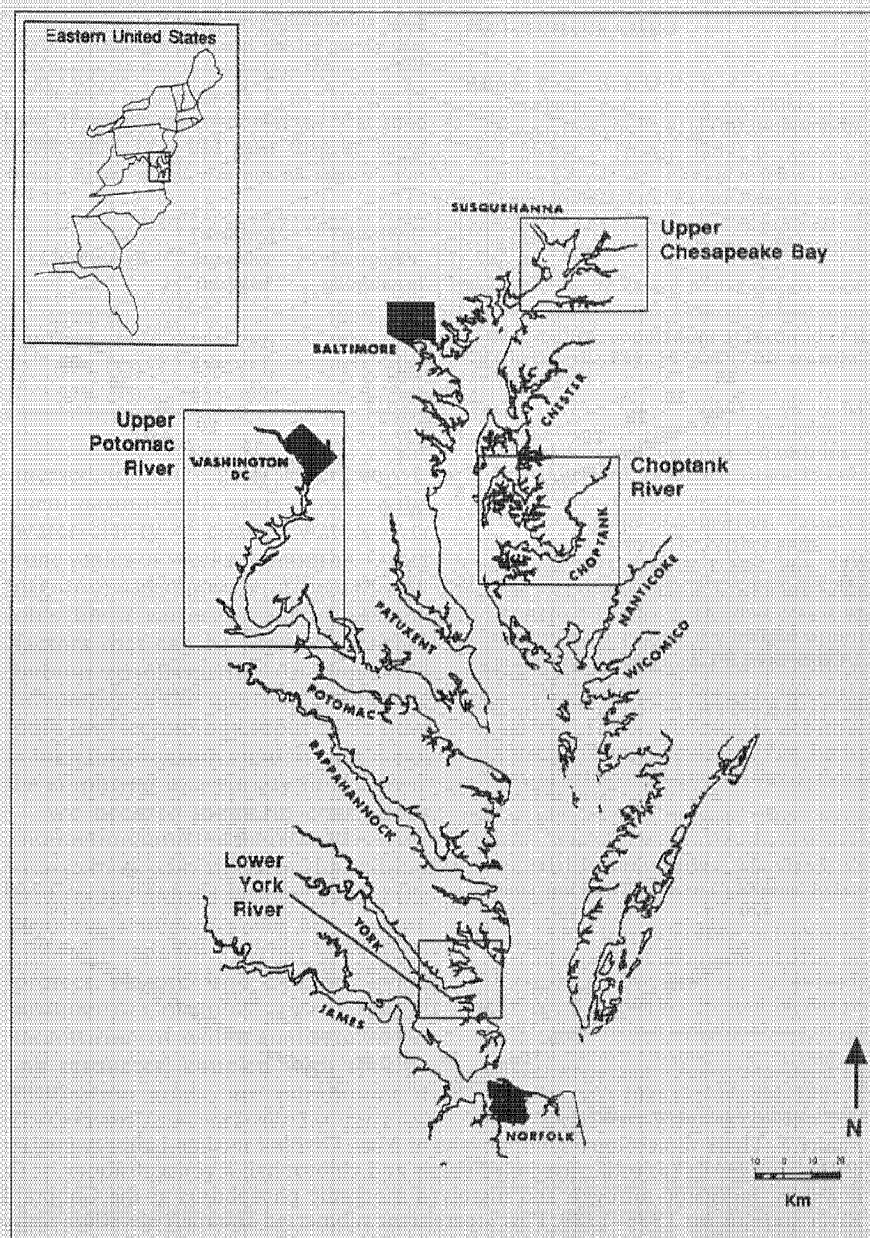


Figure 4. Chesapeake Bay with locations of the four regional study areas: Upper Chesapeake Bay, Upper Potomac River, Choptank River, and Lower York River.

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Habitat requirements for dissolved inorganic nitrogen and phosphorus varied substantially between salinity regimes. In tidal freshwater and oligohaline regions, established submersed aquatic vegetation beds sur-

vive both episodically and chronically high dissolved inorganic nitrogen; consequently, habitat requirements for dissolved inorganic nitrogen were not determined for these regions. In contrast, maximal dissolved inorganic nitrogen concentrations of $10 \text{ } \mu\text{M}$ were established for mesohaline and polyhaline regions. The submersed aquatic vegetation habitat requirement for dissolved inorganic phosphorus was less than $0.67 \text{ } \mu\text{M}$ for all regions except for mesohaline regions (less than $0.33 \text{ } \mu\text{M}$).

Differences in nutrient habitat requirements in different regions of

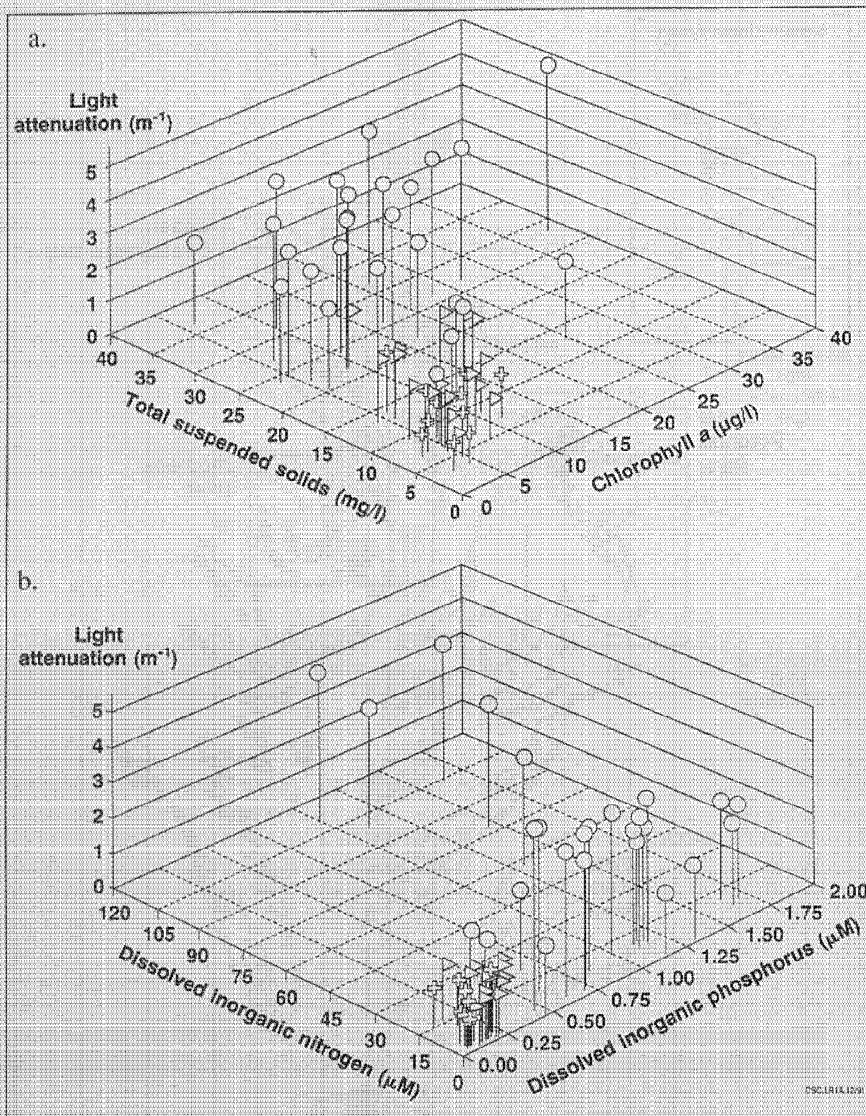


Figure 5. Three-dimensional comparisons of May–October median light attenuation coefficient versus (a) total suspended solids and chlorophyll *a* concentrations or (b) dissolved inorganic nitrogen and dissolved inorganic phosphorus at the Choptank River stations for 1986–1989. Plus = persistent submersed aquatic vegetation; flag = fluctuating submersed aquatic vegetation; circle = no submersed aquatic vegetation.

Chesapeake Bay are consistent with observations from a variety of estuaries that shifts occur in the relative importance of phosphorus versus nitrogen as limiting factors (e.g., Valiela 1984). Because habitat requirements for nutrient concentrations depended on location (e.g., freshwater versus marine), nutrient reduction strategies could vary depending on the salinity regime. However, nutrient loading in freshwater or oligohaline regions of the estuary affects nutrient concentrations of other salinity regimes, and nutrient reduction strategies may need to be baywide to achieve habitat re-

quirements in each salinity regime.

Habitat requirements can be used to generate distribution and abundance targets for restoration efforts in Chesapeake Bay. Increased water clarity would be required for submersed aquatic vegetation to penetrate to depths greater than one meter. Using a minimal light requirement of 20% (e.g., *Zostera marina*), monthly median light attenuation coefficients of 0.80 m^{-1} and 0.54 m^{-1} would be required for revegetation to maximal depths of 2 and 3 m, respectively. Combining these depth limits with Chesapeake Bay hydrography provides

estimates of potential vegetation habitat that could be compared to measured distributions, thus providing a quantitative method to assess the relative success of Chesapeake Bay restoration efforts.

Chesapeake Bay habitat requirements for submersed aquatic vegetation developed in the four study areas were applied to the rest of the bay to test the correspondence of submersed vegetation distributions with the five water quality parameters (Table 3). Chesapeake Bay was divided into 47 segments, and median water-quality values were determined in each segment using Chesapeake Bay Basin Monitoring data for each year between 1984 and 1990. Between 79% and 100% of the segments with at least 25 ha of submersed aquatic vegetation met the habitat requirements for the respective salinity regime given in Table 2.

The various water quality parameters have differing abilities to predict submersed aquatic vegetation distributions: chlorophyll *a* (99%), dissolved inorganic phosphorus (95%), light attenuation coefficient (90%), total suspended solids (84%), and dissolved inorganic nitrogen (83%); however, the overall average (90%) for all parameters is fairly high and indicates the utility of this approach.

There are few tidal freshwater and no oligohaline stations with more than 25 ha of submersed aquatic vegetation outside the upper Potomac River, so testing the habitat requirements in these areas was less intensive. The upper Potomac River was not included in this treatment because the well-established submersed aquatic vegetation populations were able to withstand occasional departures from the established distribution (Batiuk et al. in press).

The habitat requirements represent the absolute minimal water-quality characteristics necessary to sustain plants in shallow water. As such, exceeding any of the five water-quality characteristics seriously compromises the chances of submersed aquatic vegetation survival. Improvements in water clarity and nutrient reduction to achieve greater depth penetration of submersed aquatic vegetation would also increase submersed aquatic vegetation density, biomass, and distribution (Carter and Rybicki 1990,

Table 3. Application of Chesapeake Bay submersed aquatic vegetation habitat requirements using distributions and water quality data from 1984–1990. Percentages represent the frequency that submersed aquatic vegetation is present when growing season median water quality values are less than the habitat requirements listed in Table 2. Number in parentheses is the number of Chesapeake Bay segments and years with at least 25 ha of submersed aquatic vegetation distribution used to determine percentages. No oligohaline areas had more than 25 ha of vegetation, with the exception of the upper Potomac River, which was not included in this analysis.

Salinity regime	Light attenuation coefficient	Total suspended solids	Chlorophyll <i>a</i>	Dissolved inorganic nitrogen	Dissolved inorganic phosphorus
Tidal freshwater	100% (7)	100% (7)	100% (7)	—	100% (7)
Mesohaline	86% (57)	81% (59)	100% (57)	79% (57)	93% (57)
Polyhaline	94% (32)	88% (32)	97% (31)	91% (31)	97% (32)
Total	90% (96)	84% (96)	99% (95)	83% (89)	95% (96)

Dennison 1987). In addition, improvements of water quality beyond the habitat requirements could lead to the maintenance or reestablishment of a diverse population of native submersed species, with likelihood of long-term survival. Habitat requirements provide a guideline for mitigation efforts involving transplants of submersed aquatic vegetation. If habitat requirements are not met, reestablishment of plant communities via transplant efforts are futile.

Conclusions

The analyses presented here represent a first attempt at linking habitat requirements for a living resource (submersed aquatic vegetation) to water quality standards in an estuarine system. This habitat requirements approach, although deviating from the traditional dose/response measures and direct toxicity studies, provides testable hypotheses concerning water quality/vegetation interactions that can be explored in future studies in other estuaries and perhaps lacustrine systems as well. Additional experimental evidence coming from field and laboratory studies to test the empirical relationships could lead to improved predictive capability of habitat requirements.

The empirical approach used in this study allows for predictive capability without detailed knowledge of the precise nature of vegetation/water quality interactions. Because submersed aquatic vegetation are disappearing rapidly on a global scale, there is a need to provide guidelines on water quality before a more complete understanding of the complex ecological interactions is reached. Sub-

mersed aquatic vegetation are convenient natural light meters, integrating water clarity of coastal waters over time scales of weeks to months. Other organisms also possess critical thresholds for a variety of environmental factors that can be used to establish habitat requirements. An important advantage of this approach, requiring only low technology input to achieve a high information yield, is that it can be employed in a variety of settings.

We need to maintain continuous interactions and feedback between the researchers who develop the habitat criteria for individual species and the resource managers who are responsible for regulations that ultimately protect, restore, and enhance living resources. Continued research and monitoring of water quality and living resources, coupled with specific restoration goals, are paramount if these resources are to be part of humanity's future.

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References cited

- Batiuk, R. A., R. J. Orth, K. A. Moore, W. C. Dennison, J. C. Stevenson, L. Staver, V. Carter, N. Rybicki, R. E. Hickman, S. Kollar, S. Bieber, P. Heasley, and P. Bergstrom. In press. *Chesapeake Bay Submersed Aquatic Vegetation Habitat Requirements and Restoration Goals: A Technical Synthesis*. US EPA, Chesapeake Bay Program, Annapolis, MD.
- Bayley, S., V. D. Stotts, P. F. Springer, and J. Steenis. 1978. Changes in submersed aquatic macrophyte populations at the head of the Chesapeake Bay, 1958–1974. *Estuaries* 1: 171–182.
- Borum, J. 1983. The quantitative role of macrophytes, epiphytes, and phytoplankton under different nutrient conditions in Roskilde Fjord, Denmark. Pages 35–40 in *Proceedings of the International Symposium on Aquatic Macrophytes*. Faculty of Science, Nijmegen, The Netherlands.
- Cambridge, M. L., and A. J. McComb. 1984. The loss of seagrass in Cockburn Sound, Western Australia. I. The time course and magnitude of seagrass decline in relation to industrial development. *Aquat. Bot.* 20: 229–243.
- Canfield, D. E., K. A. Langeland, S. B. Linde, and W. T. Haller. 1985. Relations between water transparency and maximum depth of macrophyte colonization in lakes. *J. Aquat. Plant Manage.* 23: 25–28.
- Carter, V., and N. B. Rybicki. 1986. Resurgence of submersed aquatic macrophytes in the tidal Potomac River, Maryland, Virginia and the District of Columbia. *Estuaries* 9: 368–375.
- . 1990. Light attenuation and submersed macrophyte distribution in the tidal Potomac River and estuary. *Estuaries* 13: 441–452.
- Carter, V., J. E. Paschal Jr., and N. Bartow. 1985. Distribution and abundance of submersed aquatic vegetation in the tidal Potomac River and estuary, Maryland and Virginia, May 1976 to November 1981. US Geological Survey Water Supply Paper 2234-A.
- Chambers, P. A., and J. Kalff. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi depth. *Can. J. Fish. Aquat. Sci.* 42: 701–709.
- Champ, M. A., G. A. Gold, W. E. Bozzo, S. G. Ackelson, and K. C. Vierra. 1980. Characterization of light extinctions and attenuation in Chesapeake Bay, August 1977. Pages 263–277 in V. S. Kennedy, ed. *Estuarine Perspectives*. Academic Press, New York.
- Costa, J. E. 1988. Distribution, production and historical changes in abundance of eelgrass (*Zostera marina*) in Southeastern Massachusetts. Ph.D. dissertation, Boston University, Boston, MA.
- Cumming, H. W. 1916. Investigation of the pollution and sanitary conditions of the Potomac watershed. Treasury Department and US Public Health Service Hygienic Laboratory Bulletin no. 104.
- Davis, F. W. 1985. Historical changes in submersed macrophyte communities of upper Chesapeake Bay. *Ecology* 66: 981–993.
- den Hartog, C. 1970. *Seagrasses of the World*. North-Holland, Amsterdam, The Netherlands.

- lands.
- Dennison, W. C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat. Bot.* 27: 15-26.
- Duarte, C. M. 1991. Seagrass depth limits. *Aquat. Bot.* 0: 363-377.
- Funderburk, S. L., S. J. Jordan, J. A. Mihursky, and D. Riley, eds. 1991. *Habitat Requirements for Chesapeake Bay Living Resources*. Chesapeake Research Consortium, Solomons, MD.
- Giesen, W. B. J. T., M. M. van Katwijk, and C. den Hartog. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat. Bot.* 37: 71-85.
- Hanson, P. J., J. G. Isebrands, and R. E. Dickson. 1987. Carbon budgets of *Quercus rubra* L. seedlings at selected stages of growth: influence of light. Pages 269-276 in R. L. Hay, F. W. Woods, and H. DeSelm, eds. *Proceedings of the Central Hardwood Forest Conference VI*. University of Tennessee, Knoxville.
- Haramis, G. M., and V. Carter. 1983. Distribution of submersed aquatic macrophytes in the tidal Potomac River. *Aquat. Bot.* 15: 65-79.
- Horton, T., and W. M. Eichbaum. 1991. *Turning the Tide: Saving the Chesapeake Bay*. Island Press, Washington, DC.
- Hurley, L. 1990. *Field Guide to the Submerged Aquatic Vegetation of Chesapeake Bay*. US Fish and Wildlife Service, Chesapeake Bay Program, Annapolis, MD.
- Hutchinson, G. E. 1975. *A Treatise on Limnology*. vol. 3. *Limnological Botany*. John Wiley & Sons, New York.
- Jaworski, N. A., D. W. Lear, and O. Villa. 1972. Nutrient management in the Potomac estuary. Pages 246-273 in G. E. Likens, ed. *Nutrients and Eutrophication: The Limiting Nutrient Controversy*. American Society of Limnology and Oceanography, Lawrence, KS.
- Kautsky, N., H. Kautsky, U. Kautsky, and M. Waern. 1986. Decreased depth penetration of *Fucus vesiculosus* (L.) since the 1940s indicates eutrophication of the Baltic Sea. *Mar. Ecol. Prog. Ser.* 28: 1-8.
- Kemp, W. M., W. R. Boynton, R. R. Twilley, J. C. Stevenson, and J. C. Means. 1983. The decline of submersed vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. *Mar. Technol. Soc. J.* 17: 78-89.
- Kemp, W. M., W. R. Boynton, R. R. Twilley, J. C. Stevenson, and L. G. Ward. 1984. Influences of submersed vascular plants on ecological processes in upper Chesapeake Bay. Pages 367-394 in V. S. Kennedy, ed. *Estuaries as Filters*. Academic Press, New York.
- Kenworthy, W. J., and D. E. Haunert, eds. 1991. The light requirements of seagrasses: proceedings of a workshop to examine the capability of water quality criteria, standards and monitoring programs to protect seagrasses. NOAA Technical Memorandum NMFS-SERC-287.
- Larkum, A. W. D., A. J. McComb, and S. A. Shepherd, eds. 1989. *Biology of Seagrasses: A Treatise on the Biology of Seagrasses With Special Reference to the Australian Region*. Elsevier, New York.
- Little, M. M., D. S. Little, S. M. Blair, and J. N. Norris. 1985. Deepest known plant life discovered on an uncharted seamount. *Science* 227: 57-59.
- Luning, K., and M. J. Dring. 1979. Continuous underwater light measurement in the sublittoral region. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 32: 403-424.
- McRoy, C. P., and C. Helfferich, eds. 1977. *Seagrass Ecosystems: A Scientific Perspective*. Marcel Dekker, New York.
- Orth, R. J., and H. Gordon. 1975. Remote sensing of submersed aquatic vegetation in the lower Chesapeake Bay, Virginia. Final Report, NASA-10720.
- Orth, R. J., and K. A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submersed aquatic vegetation. *Science* 222: 51-53.
- . 1984. Distribution and abundance of submersed aquatic vegetation in Chesapeake Bay: an historical perspective. *Estuaries* 7: 531-540.
- Orth, R. J., J. F. Nowak, A. A. Frisch, K. Kiley, and J. Whiting. 1991. Distribution of submersed aquatic vegetation in the Chesapeake Bay and tributaries and Chincoteague Bay—1990. US EPA, Chesapeake Bay Program, Annapolis, MD.
- Osmond, C. B., M. P. Anstett, J. A. Berry, W. D. Billings, J. S. Boyer, J. W. H. Dacey, P. S. Nobel, S. D. Smith, and W. E. Winner. 1987. Stress physiology and the distribution of plants. *BioScience* 37: 38-48.
- Ostenfeld, C. H. 1908. On the ecology and distribution of the grass-wrack (*Zostera marina*) in Danish waters. Report of the Danish Biological Station, Copenhagen, Denmark.
- Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. *Biological Oceanographic Processes*. Pergamon Press, Oxford, UK.
- Phillips, R. C., and C. P. McRoy, eds. 1980. *A Handbook of Seagrass Biology: An Ecosystem Perspective*. Garland, New York.
- Pierce, J. W., D. L. Correll, B. Goldberg, M. A. Faust, and W. H. Kline. 1986. Response of underwater light transmittance in the Rhode River estuary to changes in water-quality parameters. *Estuaries* 9: 169-178.
- Sand-Jensen, K. 1988. Minimum light requirements for growth in *Ulva lactuca*. *Mar. Ecol. Prog. Ser.* 50: 187-193.
- Stevenson, J. C. 1988. Comparative ecology of submersed grass beds in freshwater, estuarine, and marine environments. *Limnol. Oceanogr.* 33: 867-893.
- Stevenson, J. C., and N. M. Confer. 1978. Summary of available information on Chesapeake Bay submersed vegetation. US Fish and Wildlife Service, Office of Biological Services FWS/OBS-78/66.
- Stevenson, J. C., L. W. Staver, and K. W. Staver. In press. Water quality associated with survival of submersed aquatic vegetation along an estuarine gradient. *Estuaries*.
- Thayer, G. W., D. A. Wolfe, and R. B. Williams. 1975. The impact of man on seagrass systems. *Am. Sci.* 63: 288-296.
- Twilley, R. R., W. M. Kemp, K. W. Staver, J. C. Stevenson, and W. R. Boynton. 1985. Nutrient enrichment of estuarine submersed vascular plant communities. I. Algal growth and associated effects on production of plants and associated communities. *Mar. Ecol. Prog. Ser.* 23: 179-191.
- Valiela, I. 1984. *Marine Ecological Processes*. Springer-Verlag, New York.
- Wetzel, R. G. 1975. *Limnology*. W. B. Saunders, New York.
- Williams, S. L., and W. C. Dennison. 1990. Light availability and diurnal growth of a green macroalga (*Caulerpa cupressoides*) and a seagrass (*Halophila decipiens*). *Mar. Biol.* 106: 437-443.

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